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Post-fire successions of Collembola in lowland heaths in South-Eastern UK

P. J. A. Shaw

Dept Environmental Studies, Roehampton Institute, Southlands College, Wimbledon Parkside, London SW19 5NN, UK.

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Summary. Collembola were extracted from soil samples from three lowland heath sites in south-east England. All sites were dominated by heather last burned in 1976. At two sites there had been recent fires, while at the third had recently undergone mechanical soil removal, giving a range of successional stages. A total of 25 species of Collembola were identified, with at least one species being unique to each site. Principal components ordination showed that the greatest source of variation was the community difference between an urban heath on a non-podzolic soil and the communities found on long-established heaths on podzols. Within each site the greatest source of variance was the difference between burnt and unburnt sites. Burnt sites contained a depauperate community but contained species not found on unburnt sites. High population densities (dominated by immature Collembola) were found on a burnt site within 8 weeks of a shallow fire. The possibility is mooted that fires may cause an enhanced egg germination of some Collembola.

Key words: Collembola, heathlands, fire sites, succession, eggs, seedbank

Introduction

Collembola are the second commonest group of soil arthropods after the mites (Hale 1967), and lowland heaths are among the best studied and most endangered of UK ecosystems (Gimingham 1972; Nature Conservancy Council 1984; Webb 1986). However, there appears to be no published research on the Collembola of British lowland heaths, and only few relevant publications from other European heathlands. Piart & Duvia (1985) studied Collembola on a French lowland heath before and after spreading of crushed refuse on the site, and Petersen (1995) studied Collembola on Danish heathland undergoing reversion to heathland after 2 years of arable farming. Usher et al. (1982) briefly mentioned the Collembola of a *Polytrichum* site in the North York Moors after chemical perturbation, while Newton & Pugh Thomas (1979) studied the distribution of Collembola around a path on a *Calluna* moorland in the Pennines.

Heathlands are not a true climax community, but require regular drastic intervention to knock back colonisation by trees (Webb 1986). Traditionally heathlands were maintained by grazing and turf cutting (Tubbs 1991), but the most practical method of heath management involves

E-mail: peters@max.roeham.ac.uk

controlled burning on a 15–20 year rotation. It might be expected that the fire cycle would have a profound impact on the soil arthropod community, and that the recovery of vegetation would be accompanied by a corresponding recovery of soil arthropods. Webb (1994) studied post-fire successions in cryptostigmatid mites in lowland heaths, and found that although the maximum surface temperature during a fire was lethal, below 1cm depth the soil afforded adequate thermal protection. He attributed post-fire changes in deep dwelling arthropods to changes in microclimatic conditions consequent on the loss of vegetation cover. Three months after burning most species of insect and spiders have been found to be present at normal densities in open, burnt zones although a few taxa were at highest density at the burnt/unburnt interface (Gardner & Usher 1989; Usher & Smart 1988). No species were found to be confined to the burnt sites.

Given that vegetation removal by fire causes a dramatic decrease in surface humidity (Barclay-Estrup 1971) and the known sensitivity of most Collembola to desiccation, it would be expected that post-fire changes in Collembola communities should be dramatic. The absence of work on this field constitutes a lacuna in the understanding of heathland ecology. The work described below had two goals; to define the Collembola of the plagio-climax stage of selected lowland heaths, and to examine the community changes associated with fire sites.

Materials and Methods

Site description

Work was undertaken at three lowland heaths sites; Thursley Common (UK grid reference SU906405), Headley Heath (TQ200535), and Wimbledon Common (TQ233726). Thursley Common and Headley Heath are classic examples of south eastern lowland heath on podzolic soils with extensive areas of ling *Calluna vulgaris* (L.) (Gibbons 1994; Shaw et al. 1995). Wimbledon common has a complex history (Johnson 1912; Plastow 1986), and supports a few hectares of *C. vulgaris* heath on an acidic, sandy but non-podzolised soil. None of these sites has any record of prior Collembola surveys, although information exists for the Acarina of Headley Heath (Hyatt 1990).

All three sites suffered severe fires during 1976, and the subsequent *C. vulgaris* regrowth dominates the sites, with an understorey of *Hypnum cupressiforme*. The Wimbledon Common 1976 regrowth contains small patches of *Festuca rubra* L., *Deschampsia flexuosa* (L.) Trin. and *Nardus stricta* L., and is c. 20 m from woodland dominated by *Betula* spp, mixed with *Quercus robur* L. and *Salix* spp. The Headley and Thursley sampling sites were almost pure *C. vulgaris*, with scattered *Ulex europaeus* L. bushes and an understorey of *H. cupressiforme* 2–5 cm deep.

Wimbledon Common suffered a small (0.5 ha) fire in August 1995, which caused superficial charring and removal of *C. vulgaris* stems but was followed by rapid regrowth of grasses (mainly *F. rubra* and *D. flexuosa*). Thursley experienced a severe fire over ten hectares in 1990, on which the sampled area consisted of *C. vulgaris* with patches of *Polytrichum* spp. and *Cladonia* spp. Thursley Heath also experienced a smaller (1 hectare) deep-burning fire in 1994, which remained as bare charcoal throughout the study period. Headley heath had no further documented fires, but as part of a conservation management programme in 1995, topsoil was scraped off five hectares of land leaving the bare sandy Ea horizon. Thus Wimbledon Common and Headley Heath contained two seral stages (mature heather and newly cleared areas), and while Thursley contained three (mature, 5–6 years old, and 1–2 years old).

Sampling methods

Soil cores were removed from randomly selected areas at each site using a 9 cm internal diameter steel corer (Shaw 1985), and immediately wrapped in plastic film for return to the laboratory. Once returned, cores were divided into 0–3 cm and 3–6 cm layers, and subjected to extraction in a standard Tullgren funnel. Collembola were identified using Gisin (1960) and Fjellberg (1982), and nomenclature follows Fjellberg (1982). Problematic specimens were identified by A. Fjellberg (pers. comm.) Sampling started in July 1994 and continued at intervals of approximately 2 months until the end of December 1995. The burnt/scraped sites were only sampled from July 1995 onwards.

A subsample of 0–3 cm soil cores from each site were retained for chemical analysis. Organic matter was calculated from mass loss after ignition in a muffle furnace at 400 °C. pH was measured for a 10 g: 25 ml mix of soil and distilled water on a Gallenkamp pH stick PHK 120B. Soil was air dried, sieved

(60 m mesh sieve), and extracted with 2.5% acetic acid for K and P analysis. Potassium was analysed by atomic absorbtion spectroscopy calibrated against solutions of potassium chloride. Phosphorus was determined by colorimetry using the molybdate blue method (Allen 1990).

Statistical methods

Due to the highly clumped distributions typical of Collembola, all inferential tests used on raw population data were non-parametric; Kruskal-Wallis ANOVA and Spearman's rank correlation coefficient. The population data were simplified by ordination using principal components analysis, and ordinated scores were analysed using one way analysis of variance followed by Duncan's multiple range test.

Results

Between-sites variation in mature heather communities

On the old heather (dating from the 1976 fires) a total of 22 species of Collembola were recorded (Table 1). It appears that there were substantial inter-site differences despite the similarity in age and composition of the heather. In particular, *Lepidocyrtus cyaneus* Tullberg was common and distinctive on Wimbledon commmon but was not recorded elsewhere, a pattern repeated by *Ceratophysella denticulata* Bagnall and *Orchesella flavescens* (Bourlet). By contrast, *Neanura muscorum* Templeton, *Tullbergia callipygos* Borner and (with the exception of 1 dark individual) both colour morphs of *Pseudisotoma sensibilis* (Tullberg) were found at both Thursley and Headley but not at Wimbledon.

Table 1. Densities of all Collembola in 19 year old heather on three lowland heath sites (animals m^{-2}, mean ± standard error), significance of inter-site differences using the Kruskal-Wallis test, and eigenvector loadings on the first axis of a principal components analysis

	Headley Heath	Thursley Heath	Wimbledon Common	Site Effect?	Eigen-vector 1
Anurida pygmaea	19 ± 8	22 ± 15	32 ± 28	NS	
Arrhopalites pygmaeus	0	26 ± 11	5 ± 5	*	
Ceratophysella denticulata	0	0	52 ± 23	*	+0.776
Dicyrtoma fusca	0	57 ± 23	0	**	–0.309
Entomobrya nivalis	15 ± 9	7 ± 5	111 ± 39	*	+0.474
Folsomia quadrioculata	11 ± 9	292 ± 97	2365 ± 486	**	+0.936
Friesea mirabilis	735 ± 271	618 ± 153	1620 ± 352	NS	+0.672
Isotoma viridis	33 ± 29	48 ± 23	59 ± 31	NS	+0.481
Lepidocyrtus curvicollis	0	56 ± 50	0	NS	–0.167
Lepidocyrtus cyaneus	0	0	428 ± 125	**	+0.816
Lepidocyrtus lanuginosus	95 ± 55	276 ± 71	26 ± 13	**	–0.370
Neanura muscorum	4 ± 3	24 ± 8	0	**	
Orchesella cincta	15 ± 11	8 ± 8	1 ± 1	NS	
Orchesella flavescens	0	0	16 ± 12	NS	
Pseudisotoma sensibilis					
dark morph	319 ± 124	162 ± 93	2 ± 2	*	–0.502
pale morph	122 ± 42	0	0	**	–0.437
Sminthurides spp.[1]	48 ± 34	397 ± 176	586 ± 201	NS	+0.565
Sminthurus viridis	20 ± 10	0	46 ± 32	NS	
Tomocerus longicornis	210 ± 85	64 ± 33	79 ± 38	NS	–0.102
Tomocerus minor	2 ± 2	0	0	NS	
Tullbergia callipygos	166 ± 87	600 ± 421	0	**	–0.290
Tullbergia sp[2]	916 ± 323	2893 ± 1309	672 ± 147	NS	–0.216
Total abundance:	2730 ± 541	5550 ± 2024	6100 ± 1118	NS	

[1] These were mainly *S. schoetii*

[2] These were mainly *T. macrochaeta*, but included some *T. yoosi* and immature *T. callipygos*.

Not recorded in the table was one solitary individual of the myrmecophilous species *Cyphoderus albidus* from 19 year old heather at Thursley Common

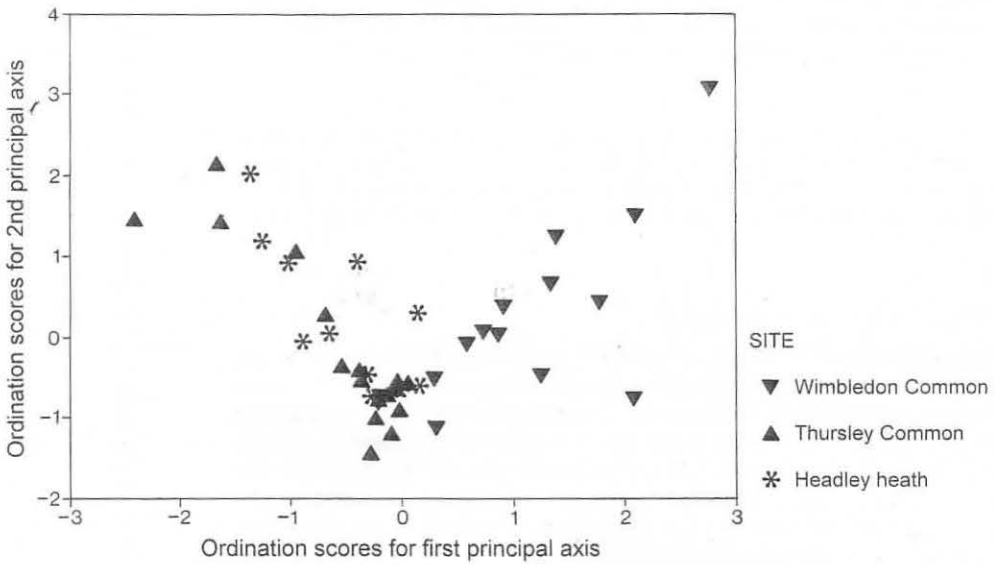

Fig. 1. The Principal Components Ordination of Collembolan communities from three lowland heaths

The data for the 15 species which occurred at densities above 50 animals per square metre in any one habitat were ordinated using principal components analysis (Gauch 1982). The first axis of the ordination accounted for 28.1 % of the variance, and the eigenvector loadings are given in Table 1. This axis corresponded to the difference between the Wimbledon Common community and that on the other two heaths (Fig. 1). Scores for Wimbledon common differed significantly ($p < .001$) from the other two sites which were not significantly different from one another. Species with large positive loadings were confined to, or commonest at, the Wimbledon Common site, while negative loadings indicated the opposite trend (Table 1).

Within-sites variation associated with disturbance

The species list for the disturbed areas is depauperate compared with that found in mature heather, but contained four species not found in any of the mature heather samples (Table 2). Of particular note is the occurrence of the uncommon sminthurid *Sminthurides lawrencii* (Gisin), which occurred in every core from the bare charcoal area at Thursley Common but was found nowhere else in the sampling programme. The newly burnt area at Wimbledon Common produced many small specimens of *Brachystomella parvula* (Schäffer) and *Lepidocyrtus cyaneus* when sampled 8 weeks after the fire, as well as mature individuals of *Onychiurus procampatus* Gisin. The scraped area at Headley Heath contained very few Collembola, but those present included *Folsomia candida* (Willem) which was found nowhere else in the survey.

A separate PCA was run for each site in turn, ordinating the species data for Collembola occurring at >50 animals m^{-2}. These ordinations are not presented, but in each case the first axis of the ordination was found to correspond to the difference between mature and disturbed sites ($p < 0.01$ by ANOVA). When first axis scores for each were analysed for disturbance effects separately by depth, the surface communities (0–3 cm) differed in all cases while the subsurface communities (3–6 cm) did not.

Table 2. Densities of Collembola on newly disturbed heathland sites, mean ± standard error. Species followed by * were not found in any of the samples from mature heather. Abbreviations: M = mechanical disturbance (removal of upper soil layers), F = fire

Site:	Headley Heath	Thursley Common	Thursley Common	Wimbledon Common
Year of disturbance:	*1995*	*1990*	*1994*	*1995*
Nature of disturbance:	M	F	F	F
Anurida pygmaea	0	27 ± 19	28 ± 20	4 ± 4
Arrhopalites pygmaeus	0	22 ± 8	66 ± 28	4 ± 4
*Brachystomella parvula**	0	0	0	267 ± 248
Entomobrya nivalis	13 ± 7	16 ± 10	29 ± 10	67 ± 53
Folsomia quadrioculata	0	60 ± 38	0	270 ± 99
*Folsomia candida**	278 ± 185	0	0	0
Folsomia inoculata	0	0	0	4 ± 4
Friesea mirabilis	0	7 ± 5	530 ± 267	290 ± 122
Ceratophysella denticulata	118 ± 45	0	0	220 ± 97
Isotoma viridis	0	0	8 ± 5	8 ± 8
Lepidocyrtus cyaneus	0	0	0	527 ± 225
Lepidocyrtus lanuginosus	0	2 ± 2	0	4 ± 4
*Onychiurus procampatus**	0	0	0	259 ± 131
Pseudisotoma sensibilis dark morph	0	228 ± 115	0	8 ± 5
Sminthurides spp.[1]	0	801 ± 433	57 ± 37	51 ± 51
*Sminthurinus lawrencei**	0	0	330 ± 115	0
Sminthurus viridis	0	17 ± 12	0	4 ± 4
Tullbergia callipygos	0	42 ± 42	14 ± 14	0
Tullbergia sp[2]	229 ± 120	235 ± 86	1254 ± 558	63 ± 30
Total abundance:	638 ± 114	1457 ± 369	2316 ± 580	1783 ± 743

Chemical tests on soils

Data for soil samples taken under 19 year old heather at each site are given in Table 3, which shows inter-site differences to be significant for all parameters measured with Thursley Common having the lowest values in each case. Burning increased the pH at both Thursley and Wimbledon, but only affected the organic matter content at Thursley Common (Table 3).

Discussion

The data presented above contain two themes; community variation between sites for comparable aged stands of *Calluna vulgaris*, and within-site variation due to burning or mechanical disturbance. The between-site variation is dominated by differences between the community at Wimbledon Common and those on the other two heaths (Fig. 1, Table 1). This contrast is reflected in the soil profiles. Wimbledon common is not podzolic, being closer to a forest brown earth, whereas the other two sites support typical heathland podzols. These results raise the possibility that Collembola may act as ecological indicators of ancient heathlands in the same way that some plants can indicate ancient woodland (Peterken 1974).

Although there is little work published on Collembola of British lowland heaths, the species list can be compared with data for continental European heaths, and for upland heaths in the UK. Four species overlap with the lists of Usher (1976) and Shaw & Usher (1995); *Folsomia quadrioculata* (Tullberg), *Friesea mirabilis* Dalla Torre, *Neanura muscorum* and *Pseudisotoma sensibilis*. Species common to this dataset and the results of Piart & Duviart (1985) are *Dicyrtoma fusca* (Lucas), *Sminthurides schoetti* (Axelson), *Entomobrya nivalis* L., *Lepi-*

Table 3. Summary soil chemical data, in all cases given as mean ± standard error
Part 1. Results for soils under 19 year old heather at each site, followed by the result of a 1 way ANOVA examining whether each parameter differed between the three sites. Means for each variable followed by the same letter are not significantly different at p = 0.05 by Duncan's multiple range test

Site:	*Headley Heath*	*Thursley Common*	*Wimbledon Common*	*Site effect*
pH	3.74 ± 0.05a	4.21 ± 0.03b	4.02 ± 0.09c	**
LOI	68.77 ± 7.01a	16.87 ± 1.77b	45.24 ± 8.43c	**
K	23.38 ± 1.16a	5.78 ± 0.66b	28.53 ± 1.01c	**
P	4.45 ± 0.32a	0.71 ± 0.19b	6.80 ± 0.77c	**

Part 2. Results for soils from disturbed areas. Data for each site are followed by the result of a 1 way ANOVA examining whether disturbed soils differed from undisturbed areas at the same site

Site:	*Headley Heath*	*Thursley Common*	*Wimbledon Common*
pH	3.59 ± 0.03 *–	4.81 ± 0.03 **+	4.41 ± 0.09 **+
LOI	4.33 ± 0.19 **–	11.18 ± 0.27 *–	46.87 ± 8.09 NS
K	4.71 ± 0.27 **–	3.69 ± 0.59 *–	24.52 ± 3.54 NS
P	0.18 ± 0.01 **–	0.56 ± 0.11 NS	3.76 ± 0.15 **–

Abbreviations: P; Available phosphorus (mg 100 g^{-1}), K; Available potassium (mg 100 g^{-1}), LOI; % mass loss on ignition, NS; $p > 0.05$, *; $p < 0.05$, **; $p < 0.01$, + indicates an increase with respect to undisturbed soil, – indicates a decrease with respect to undisturbed soil

docyrtus cyaneus, *L. lanuginosus* (Gmelin), *Orchesella cincta* L., *Isotoma viridis* Bourlet, *Neanura muscorum* and *Ceratophysella denticulata*. Species overlapping with the results of Petersen (1995) are *Anurida pygmaea* Borner, *Tullbergia macrochaeta* Rusek, and *Orchesella cincta*.

The degree of species overlap may be higher than apparent due to taxonomic problems; Petersen (1995) recorded *Isotoma anglicana* Lubbock and *Entomobrya multifasciata* Tullberg, which if found in the present survey would have been recorded as *I. viridis* and *E. nivalis*. In both cases the taxonomic split is uncertain (Fjellberg 1982), and the more conservative name was used in the species lists given above. In addition, Petersen (1995) does not give a complete species list, with only the commonest 12 species named out of approximately 40 taxa recorded. Piart & Duviart (1985) recorded no members of the Onychiuridae at all (suggesting a deliberate policy of omission), but noted four species of *Sminthurides* including *S. schoetti* and *S. parvulus* Krausbauer, while the data presented above pooled all *Sminthurides* together due to their large numbers and the difficulty of distinguishing species under a low power microscope. In fact the specimens that were examined proved to be mainly of *S. schoetti* with a minority of *S. parvulus*. Such taxonomic problems are a recurring theme in research on the ecology of Collembola (Hopkins 1997).

The second aspect of the data concerned variation associated with burning/disturbance of sites. The disturbance at Headley heath involved gross mechanical removal of all upper soil layers, with inevitably dramatic effects on soil composition (Table 3). The burning experienced at the other two sites differed in its impact, with the Wimbledon common burn being relatively superficial compared to the deep burns at Thursley. Vegetation regrowth started at Wimbledon within 8 weeks of the fire while one site at Thursley remained bare 18 months later. This is reflected in the observation that the effect of burning on soil organic matter was significant at Thursley but not at Wimbledon (Table 3). At both sites burning increased pH, presumably due to deposition of alkaline ashes. At each site the burnt/disturbed areas supported a depauperate community, but with one or two species found nowhere else in the survey.

The scraped area at Headley heath contained *Folsomia candida*, the burnt area at Wimbledon held *Onychiurus procampatus* and *Brachystomella parvula*, while the bare charcoal at Thursley held *Sminthurides lawrencei*. This emphasises the need to maintain a habitat mosaic with a range of successional stages to optimise biodiversity of heathlands, which is in any case standard conservation policy for these sites (Tubbs 1991; Dolman 1993).

These results also raise questions about the origin of species which appear on burnt sites. Several explanations can be offered to account for the occurrence of species specifically on burnt sites. The most conservative is that they have always been present, that they survived the fire better than other species, and that their absence from unburnt sites is an artefact of a patchy spatial distribution combined with a limited sampling programme. This rather negative hypothesis may be the best explanation for the occurrence of mature *O. procampatus* on the burnt area at Wimbledon common 8 weeks after a fire. *Onychiurus* species are blind, euedaphic species capable of only slow dispersal, and could be expected to survive a shallow fire by being insulated at depth in the soil. It is noteworthy that the burnt area at Wimbledon contained a higher species richness than the other disturbed sites (Table 2), again suggesting a low impact of the fire.

An alternative explanation for the colonization by Collembola of burnt areas is recolonization from adjacent sites, coupled with "r-selected" life-cycle characteristics favouring rapid exploitation of bare habitats. The colonisation source need not be from unburnt vegetation; Bellido (1987) found that heathland fires have a high degree of spatial variability, and that islands of lightly burnt vegetation can act as sources from which soil arthropods can recolonise the surrounding charred soil surface.

This recolonization hypothesis assumes that the "fire site" species are omnipresent in unburnt habitats, but at such low population densities that they are rarely found in surveys. This model seems to be the most likely explanation for the occurrence of *S. lawrencei* on charcoal at Thursley, and *F. candida* on bare sand at Headley heath.

Finally, a tentative hypothesis may be put forward which is not proven by data presented above but which deserves consideration. This concerns the possibility that some species produce an "egg bank" in soil (analogous with plant seed banks), and that physico-chemical changes following a fire stimulate egg germination. This model would only apply to sites experiencing mild fires which leave the upper layers of the soil undamaged, and could explain the occurrence of immature *Brachystomella parvula* and *Lepidocyrtus cyaneus* within 8 weeks of the fire on Wimbledon common. Possible triggers could be a short heat spike, or addition of high pH ash to the soil solution. This unproven hypothesis is amenable to experimental testing, and if verified would mean that Tullgren extraction of soils does not define the potential Collembola community any more than observation of a plant community can predict the composition of its soil seed bank.

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